THE ASEXUAL CYCLE OF PLANARIA VELATA IN RELATION TO SENESCENCE AND REJUVENESCENCE.

C. M. CHILD.

I. The Life Cycle under Natural Conditions.

During early spring in the region about Chicago, a planarian appears in temporary ditches and pools, particularly in those which are more or less filled with dead leaves. It is also often found in permanent bodies of water such as springs, permanent ponds and brooks, but seems to attain the greatest numbers in the temporary ditches and pools. The animal is apparently the species recently described by Stringer ('09) and named *Planaria velata*. The shape and proportions of the larger individuals are indicated in Fig. 1.

When the animals first appear soon after the ice melts they are mostly only 2–3 mm. in length and commonly light in color. They grow rapidly and soon the dorsal surface becomes very deeply pigmented so that they appear almost black. They are very active and their locomotion is much more rapid than that of most other fresh water planarians. During this period they react readily to meat of various kinds and can be collected in large numbers by placing pieces of meat in the water. In about four weeks they attain a length of 12–15 mm., their movements gradually become slower, they cease to react to food, become light gray in color from loss of pigment and sooner or later the pharynx disintegrates.

Within a few days after these changes a process of division begins. As the worms creep about, the extreme posterior end adheres to the substratum and the rest of the animal pulls away and leaves it behind as a small fragment which becomes more or less spherical and within a few moments is covered with a slime which adheres to the underlying surface and hardens into a cyst. This process of division is repeated, often several times within a few moments, so that as the animal moves across the containing vessel it may leave behind it a series of such pieces. The pieces vary considerably in size, some being as large as 1.5 mm. in diameter, some only about 0.5 mm. The process continues until half or two thirds or sometimes even more of the worm is separated into pieces and then the anterior region including the head may encyst without further division or in some cases dies.

I

Under natural conditions the encysted pieces remain quiescent during the summer and the following winter and in early spring emerge from the cysts as minute, very active worms which at once begin to feed and grow and repeat the cycle. As I have determined by experiment, the encysted pieces are not capable of withstanding desiccation and it is probable that this fact is connected with the occurrence of the worms in ditches and pools partly filled with dead leaves. In such localities even though the water disappears, the bottom under the thick layer of leaves is always more or less wet and the encysted pieces are not subjected to drying.

During the last thirteen years I have collected these worms almost every year and have never found a single individual with mature sexual organs or even any indication of sexual reproduction. Every year the active period ends with decrease in activity, cessation of feeding, loss of pigment, fragmentation and encystment of the fragments.

In this species then, under the conditions where it occurs in this locality, development and growth result in a process of senescence, the individual breaks up into fragments which undergo regulation within the cysts to small whole animals, and these are to all appearances physiologically as well as morphologically young and are capable of repeating the life cycle. In short, senescence is followed in these animals not by death but by asexual reproduction and rejuvenescence.

During a number of years I have kept a stock of these worms in the laboratory, have bred them through several asexual generations and have subjected them to various experimental conditions. The results of this asexual breeding and the experimental modifications of the life cycle will be discussed in another paper.

II. The Physiological Resistance to Depressing Agents of Young and Old Worms.

In these experiments the method of comparing resistances which I have called the direct method was used. Here the depressing agent is used in sufficiently high concentration to kill the animals within a few hours and the occurrence of death is determined by disintegration of the worms which begins within a few moments after death. This method has been fully described in another paper (Child, '13*a*). In that paper it was shown that with this method the animals with the higher rate of metabolism or more strictly of cell respiration are less resistant and therefore die and disintegrate earlier than those with the lower rate. Thus the differences in resistance enable us to compare the rates of respiration and so in a general way the rates of metabolism.

In Table I. the first vertical column gives the length of time in the depressing agent in hours and minutes, the second the serial numbers of the lots of worms compared, and the columns I.–V. under "Stages of Disintegration" give the number of worms of each lot in each stage of disintegration at each time. As regards the five stages, I have found it convenient to distinguish more or less arbitrarily these stages in the process of disintegration, for disintegration usually appears first in certain definite regions of the body while other regions are still alive and show movement and it follows a more or less regular course (Child, '13*a*). The five stages are briefly characterized as follows:

I. Intact, no disintegration.

II. Disintegration beginning, usually in head region.

III. Body beginning to disintegrate but form still retained.

IV. Margins disintegrated, form disappearing in consequence of swelling of tissues and separation of cells.

V. All epithelium and pigment gone; swelling of tissues has extended to all parts and original form has disappeared.

The distinction of these stages makes it possible to compare different lots of worms more closely than if only the time of complete disintegration were noted.

In Table I. Lot 1 consists of ten worms 1.5–2 mm. in length, which had emerged from cysts within three or four days preceding and had been fed once with pieces of earthworm after emergence. Lot 2 consists of ten worms 13–15 mm. which had been raised in the laboratory from cysts with earthworm as food and were almost ready to encyst again.

Table I.

Series 77. KCN 0.001 mol.

Length of Time in KCN.	Lots.	Stages of Disintegration.				
		I.	II.	III.	IV.	V.
1.30	1	8	1	1		
	2	10				
2.00	1	5	1		1	3
	2	10				
2.30	1	4	1			5
	2	10				
3.00	1	2	2	1		5
	2	10				
3.30	1			3		7
	2	6	3	1		
4.00	1					10
	2	3	5	1	1	
4.30	2		8	1		1
5.00	2		4	4	1	1
5.30	2		1	4	3	2
6.30	2				3	7
7.30						10

It is evident at once from the table that the resistance of the worms of Lot 1 recently emerged from cysts is very much less than that of the large worms of Lot 2. Disintegration begins in

Lot 1 after one and one half hours in KCN, while the worms of Lot 2 are still intact and slowly moving about. In Lot 2 disintegration begins after three hours. All the worms of Lot 1 are completely disintegrated after three and one half hours, those of Lot 2 after seven and one half hours, *i. e.*, the survival time of Lot 2 is nearly double that of Lot 1. In other words the worms of Lot 1 have a much higher rate of metabolism than those of Lot 2.

That the difference in size of the worms is not responsible for the difference in survival time is evident for two reasons: first in these flattened elongated animals the surface increases almost as rapidly as the volume and second the time of beginning of disintegration (Stage II.) is much later in Lot 2 than in Lot 1. The earliest stages of disintegration involve the external surface of the body and the surface of the large worms including the cilia remains alive for a much longer time than that of the small worms. Moreover, if the difference in size determined the difference in survival time we should expect that this would be much greater since the small worms are only a minute fraction of the size of the larger. The difference in the rate of the metabolic processes affected by the KCN is the only factor which will account for the results (Child, '13*a*).

Unfortunately it has thus far been impossible to compare the worms emerging from the cysts with young worms hatched from eggs because I have never observed sexual reproduction in this species, but the difference in rate of metabolism between the small and large worms is similar to the difference known to exist in other forms between young animals sexually produced and old.

It is, however, not necessary to use the extremes of the life cycle for comparison. Animals in various stages of growth may be compared and in all cases those which are nearer the stage when encystment occurs, *i. e.*, those which are older as regards growth and development, show the higher resistance.

In Table II. the survival times of a series consisting of five worms 5-6 mm. in length (Lot 1) and five worms 11-12 mm. (Lot 2) are given.

Table II.

Series 64, I., II. KCN 0.001 mol.

Length of Time in KCN.	Lots.	Stages of Disintegration.				
		I.	II.	III.	IV.	V.
2.30	1	2	3			
	2	5				
3.00	1		3	1	1	
	2	5				
3.30	1		1	2	1	1
	2	3	2			
4.00	1				1	4
	2	1	4			
4.30	1					5
	2		4	1		
5.30	2			5		
6.30	2				4	1
7.30	2					5

In this series also the younger worms show less resistance, which signifies a higher rate of metabolism, but a comparison of Table II. with Table I. shows that Lot 1 of Table II. has a longer survival time than Lot 1 of Table I., *i. e.*, worms of 5–6 mm. in length have a lower rate of metabolism than worms recently emerged from cysts. These facts show that a progressive decrease in the rate of metabolism occurs during the growth of the animals. Those newly emerged from cysts have the highest rate, those which are full-grown and nearly ready to fragment and encyst have the lowest rate, while intermediate stages show rates between these two extremes.

These results have been confirmed by various other series with both KCN and alcohol. The small newly emerged worms die much earlier in all cases than the large worms. The differences in resistance to KCN, alcohol, etc., between young and old animals are the same in animals freshly collected from their natural habitat as in animals bred for one or more generations in the laboratory.

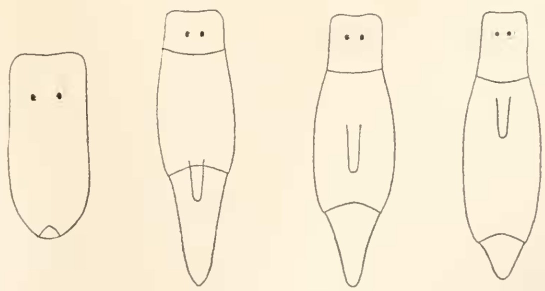
The results obtained in this way are further confirmed by the much greater activity of the small recently emerged animals. They move much more rapidly, are much more irritable and show a much higher rate of growth than the large animals. And finally the small worms from the cysts are capable, as noted in the preceding section, of repeating the life cycle. There can I think be no doubt that the worms emerging from the cysts are physiologically young and that they undergo a process of senescence as they grow in size. Evidently a process of rejuvenescence is associated in some way with the asexual reproduction which follows growth and development.

III. Experimental Reproduction.

1. *The Course of Experimental Reproduction.*

The process of reproduction of whole animals from pieces isolated by section is very similar to that in other planarians. Pieces from any region of the body and above a certain limit of size, which varies somewhat with the region, are capable of giving rise to whole animals.

As in other species of Planaria, the process consists in part of the outgrowth and differentiation of embryonic tissue from the cut surface and in part of redifferentiation of other tissues to a greater or less distance from the cut surface. In pieces of equal length the amount of anterior new tissue is greater and of posterior new tissue less in those from the anterior region of the body, while with increasing distance of the end of the piece from the head region the amount of anterior new tissue increases and



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that of posterior new tissue decreases. The development of the new head is more rapid in anterior than in posterior pieces. The position of the new pharynx is posterior to the middle in anterior and anterior to the middle in posterior pieces. Short pieces from the extreme anterior region frequently fail to develop a new posterior end. Fig. 2 shows a piece of this kind. Figs. 3, 4 and 5 show three pieces, the first from the anterior, the second from the middle and the third from the posterior region. The different amounts of new tissue produced are seen in the figures. All these graded differences, like those in *Planaria dorotocephala* (Child, '11*c*), indicate the existence of a physiological gradient of some sort along the axis. As a matter of fact this gradient is essentially similar to that which exists in *P. dorotocephala* (Child, '12, '13*c*).

2. *The Encystment of Artificially Isolated Pieces in Relation to Size of Piece and Region of Body.*

Pieces isolated by section may undergo the regulation to whole animals either with or without encystment. The frequency of encystment varies with region of the body from which the piece is taken, with the size of the piece and with the physiological age of the animal. The following records of series will serve to illustrate this. In these series a number of worms, ten, twenty or twenty-five, from the same stock and as nearly as possible of the same size and in the same physiological condition are cut into a number of as nearly as possible equal pieces, the corresponding pieces are placed together in one lot and results recorded for each piece. Since different numbers of worms are used in different series the results are given in percentages.

Series 19, April 13, 1911.—Ten worms, full grown (12–14 mm.), but still feeding and deeply pigmented. Heads removed and remainder of body cut into two equal pieces, *a*, the anterior, and *b*, the posterior. Table III. shows the percentages of the pieces which develop into whole worms without encystment and of pieces which encyst soon after the operation and emerge, from a few days to several weeks later, as whole worms after regulation in the cysts.

Table III.

	No Encystment.	Encystment.
a	90	10
b	60	40

Series 20, April 13, 1911.—Ten worms from same stock, of same size and in same condition as Series 19. Heads removed and body cut into four equal pieces, *a*, *b*, *c*, *d*, *a* being the most anterior. Table IV. gives the results.

Table IV.

	No Encystment.	Encystment.
a	90	10
b	80	20
c	30	70
d	20	80

Series 27, April 17, 1911.—Ten worms like those of Series 19 and 20 in size and condition. Heads removed and body cut into eight equal pieces, *a–h*, *a* being the most anterior. The results are given in Table V.

Table V.

	No Encystment.	Encystment.
a	20	70
b	10	90
c		100
d		100
e		100
f		100
g		100
h		100

It is evident from these three series and abundantly confirmed by numerous others, first, that the frequency of encystment of pieces increases from the anterior to the posterior end of the body and second, that the frequency of encystment increases as the size of the piece decreases. In all these series the greater frequency of encystment in more posterior pieces is evident in greater or less degree. In Series 19 where the pieces represent halves of the body the percentages of encystments are small, in Series 20, composed of $\frac{1}{4}$ pieces, they are larger except in the most anterior piece and much larger in the two posterior pieces *c* and *d* which together equal *b* of Series 19. And finally, in Series 27 which consists of $\frac{1}{8}$ pieces all the pieces encyst except 30 per cent. of *a* and 10 per cent. of *b*. When the pieces are cut still smaller all encyst.

The frequency of encystment then shows in pieces of equal size a gradation from the anterior to the posterior end of the body and indicates the existence of some sort of a physiological gradient in the animal. Encystment may, however, occur in pieces from any region if they are sufficiently small, but in general anterior pieces must be smaller than posterior pieces to give the same frequency of encystment. This fact indicates that the physiological state of the piece differs in some way with its size. As a matter of fact this species possesses essentially the same sort of gradient in rate of metabolism as *Planaria dorotocephala* (Child, '13*a*, '13*c*) and the relation between frequency of encystment, region of the body and size of the piece depends upon the existence of this gradient and the changes in rate of metabolism which occur in pieces from different regions of the body and of different size after isolation. Further consideration of these points is postponed to another time.

3. *The Frequency of Encystment of Pieces in Relation to Temperature.*

Series 53, October 5, 1911.—Animals 9–10 mm. in length were selected from a stock which had been kept at a temperature of 20° C., the heads removed and the bodies cut into four equal pieces *a–d*. Lots of ten each of each of the four pieces were placed in three different temperatures, 10°, 20° and 28–30° C. Table VI. gives the results in percentages.

It is evident at once from Table VI. that the frequency of encystment is greater with higher than with lower temperature, *i. e.*, the higher the rate of metabolism in the pieces the greater the frequency of encystment. Numerous other series give the same results without exception, not only for pieces, but for whole worms. Worms which have been kept at a temperature of 20°, when placed in a temperature of 30° will often encyst entire while at 20° they remain active until they fragment and the pieces encyst, and at 10° many of them do not encyst at all.

TABLE VI.

Temperature.	Pieces.	No Encystment.	Encystment.	Dead.
10°	*a*	100		
	b	90	10	
	c	20	80	
	d	10	90	
20°	*a*	100		
	b	70	30	
	c		100	
	d		100	
28–30°	*a*		100	
	b		100	
	c		100	
	d		100	

4. *The Frequency of Encystment in Pieces in Relation to Age.*

In the very small young worms recently emerged from cysts pieces, unless very small, usually reproduce whole worms without going through a period of encystment. As the worms increase in size and become physiologically older the frequency of encystment increases until in worms which are almost ready to fragment and encyst naturally all pieces resulting from section usually encyst.

The differences in this respect between half grown worms, worms which are about full grown but have not yet ceased to feed and still retain their dark color and worms which have stopped feeding and become gray in color are shown in the three series following.

Series 47, September 21, 1911.—Twenty worms about half grown (7 mm. in length) were cut into four equal pieces, *a–d*. The percentages of regulation without encystment and of encystments appear in Table VII.

TABLE VII.

	No Encystment.	Encystment.	Dead.
a	95		5
b	95	5	
c	55	45	
d	20	80	

Series 56 I, October 12, 1911.—Ten worms full grown but still dark in color and still feeding. Body cut into four equal pieces, *a–d*. Table VIII. gives percentages of encystments.

TABLE VIII.

	No Encystment.	Encystment.
a	60	40
b		100
c		100
d		100

Series 58 I, October 13, 1911.—Ten worms, full grown, gray in color and no longer feeding. Body cut in four equal pieces, *a–d*. Table IX. gives percentages.

TABLE IX.

	No Encystment.	Encystment.
a		100
b		100
c		100
d		100

The older worms show the greater frequency of encystment of pieces. The same results have been obtained in other similar series without exception.

5. *The Physiological Condition of Animals Reproduced from Artificially Isolated Pieces.*

The animals reproduced from pieces isolated by section are physiologically young, whether a period of encystment occurs or not. In this respect they are similar to the worms produced from the pieces which separate and encyst naturally. Small pieces cut from the bodies of old worms and allowed to reproduce whole animals show the same differences in rate of metabolism from old animals as the worms emerging from cysts naturally produced. The differences in susceptibility to cyanide are essentially the same as in Table I. Moreover, these small worms arising from pieces of large old worms are capable of rapid growth if fed and of repeating the life cycle. As they grow the rate of metabolism, as indicated by their susceptibility to cyanide, decreases, the rate of growth and the degree of activity also decrease, they finally stop feeding, lose their dark color and give rise to cysts again and from these a new generation of young worms emerges. Stocks of animals produced from pieces have passed through this cycle repeatedly in the laboratory.

The degree of rejuvenescence in this experimental reproduction varies with the size of the piece. The smaller the piece, the more extensive the reorganization and the younger the worm which results. In all respects these results are essentially the same as those obtained with *Planaria dorotocephala* and described in an earlier paper (Child, '11*b*).

It is evident also that there is no essential difference in this respect between the process of fragmentation in old worms and the reproduction of young worms from the encysted pieces in nature and the process of experimental reproduction of animals from pieces isolated by section. In nature the fragmentation occurs only in old animals by a process characteristic of a certain stage of the life cycle. In experiment the pieces can be isolated at any stage of the life history and may be of any size. In both cases the reorganization, together with the period of starvation which is also a factor as will appear, brings about rejuvenescence and the worms thus produced are capable of repeating the life history from the stage at which they begin again to feed to the stage of fragmentation.

IV. The Nature of the Process of Encystment.

It has been shown that the frequency of encystment of pieces increases with rising temperature, with decreasing size of the piece, with increasing distance of the level of the piece from the head region and with advancing age of the animals. Pieces from any region of the body may encyst if the temperature is sufficiently high, if the pieces are sufficiently small or if the animal is sufficiently old. All of these conditions must have something in common as regards their effect upon the pieces since all produce similar results. What is this common factor?

When a piece is cut from the body it is stimulated and its rate of metabolism increases. This is generally admitted but it can also be demonstrated by the cyanide method. The susceptibility to cyanide of a piece immediately after isolation is much greater than that of the corresponding region of the body in an uninjured animal of the same age and physiological condition. This greater susceptibility of the piece means that it has been stimulated by the act of isolation. After this sudden rise its susceptibility to cyanide decreases gradually during twenty-four hours or more and in small pieces may fall below that of corresponding regions in the uninjured animal (Child, '13*b*). This decreasing susceptibility means that the rate of metabolism in the piece is gradually decreasing as the stimulation resulting from section gradually disappears.

The cyanide method shows further that the degree of stimulation increases as the size of the piece isolated decreases and also as the distance of the level of the piece from the head region increases. In other words smaller or more posterior pieces are more stimulated by the act of section than larger or more anterior pieces. And finally pieces cut from worms at a higher temperature within certain limits are more stimulated and show a greater increase in rate than pieces from worms at a lower temperature.

These relations between the degree of stimulation of pieces and the factors of size of piece and region of the body and various external conditions have been worked out completely for *Planaria dorotocephala* and the data will be presented in full elsewhere. Sufficient work has been done on *P. velata* to show that the relations are essentially the same as in *P. dorotocephala*, but since the work on the latter species furnishes the foundations for the conclusions and since the data for that species are in more complete form and will be published in a short time the evidence for the above statements concerning the degree of stimulation in pieces of *P. velata* is not presented in detail.

So far then as region of the body, size of piece and temperature are concerned the frequency of encystment of pieces in *P. velata* runs parallel to the degree of stimulation by the act of section. Apparently the more the piece is stimulated by section the more likely it is to encyst.

The process of encystment in this species consists in the rapid secretion over the surface of the body of a thick slime which soon hardens into a tough membrane and forms the cyst. It is a familiar fact that stimulation is often followed in the turbellaria by the secretion of a large amount of slime. That is exactly what occurs in these pieces and in this species the slime hardens and forms the cyst. Apparently then the encystment of pieces in *Planaria velata* is simply the result of a sudden stimulation. Any factor that increases the stimulation increases the frequency of encystment.

As regards the greater frequency of encystment with advancing age of the worms, I have not been able to reach a definite conclusion based on experiment, but my observations indicate that old worms secrete more slime on stimulation than young. Apparently the gland cells either increase in number or the quantity of the substance in them which produces the slime increases as the animals grow older.

When the slime which produces the cyst first appears it is soft and an active whole animal is able to creep out of it without difficulty, but the pieces are much less active and do not succeed in escaping from it before it hardens. If the cysts are carefully opened with needles soon after they are formed and the pieces removed without injury or any great degree of stimulation they usually do not encyst again but develop into whole worms while free. But if they are injured or otherwise strongly stimulated they commonly encyst a second time.

In short all the facts indicate that encystment of pieces is merely a result of the stimulation accompanying section. It is not an adaptation to conditions or a preparation for the future in any sense. The animals do not encyst because they usually live in temporary bodies of water but they are able to live under these conditions because they encyst.

V. The Process of Fragmentation in Old Worms.

The process of fragmentation in nature is very evidently similar in character to the process of zooid-formation and fission in *Planaria dorotocephala* and *P. maculata* (Child, '11*e*). In consequence of increase in length of the body and the decrease in rate of metabolism as the animal becomes older the posterior regions of the body usually become to some extent physiologically isolated from the dominant region (Child, '11*a*, '11*d*).

That the occurrence of fragmentation is connected with a decrease in the rate of metabolism and consequent physiological isolatiion of posterior regions is clearly indicated by the fact that fragmentation may often be induced, even in worms which are not full-grown, by suddenly lowering the temperature ten to fifteen degrees. In such cases fragmentation usually begins in the posterior region within a few days.

The degree of isolation is not sufficient to permit development at once into a new individual but it is sufficient to permit some degree of independence in motor reaction, consequently, at some time when the worm is creeping the posterior end attaches itself and the rest of the body pulls away from it, as in *P. dorotocephala*. Apparently the greater part of the body in old fragmenting animals consists of a series of these small zooids for in most animals fragmentation continues until only the anterior third or fourth of the body together with the head remains. This anterior piece may then encyst or may undergo rejuvenescence without encystment and after some weeks give rise to a new posterior end, or in some cases it dies.

The posterior zooids are present only dynamically and not morphologically, at least not visibly, and they are not to be thought of as absolutely fixed stable entities. When the animal is strongly stimulated it is able to control the whole length of the body and for the time being the posterior zooids may almost or quite cease to exist, only to reappear after the stimulation is over. When such zooids are established the regions at their ends must be subjected to constantly varying correlative conditions. Sometimes they may form a physiological posterior part of one zooid, at other times an anterior part of another and at still others a part of neither. Such changes in correlative conditions must tend to weaken and eliminate the existing structure in those regions since the development of such structure depends on a certain degree of constancy in correlative factors. In this way zones of structural weakness arise and these are the zones where separation occurs.

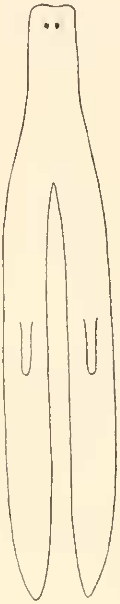
Occasionally, either in consequence of weakness or perhaps because the physiological isolation of the posterior regions is insufficient the worm fails to fragment. In such cases parts of the body may become greatly elongated and a string of connected masses may arise. Figure 6 shows such a case. In the posterior region four distinct masses can be distinguished. These are connected by slender bands which are merely portions of the body greatly reduced in diameter. These four masses are connected with the anterior portion of the body by a long slender band resulting from the stretching of the middle region in consequence of the attempts of the head region to pull away from the attached posterior parts. These greatly elongated regions of the body consist of little more than the body-wall and muscles; the alimentary tract and the parenchyma may be almost or entirely squeezed out of them. This animal finally became surrounded by a cyst in the form shown in the figure, but later the connecting strands apparently atrophied, the pieces became entirely separate and each produced a whole worm.

6

VI. The Development of the Whole Animal Within the Cyst.

The development of the animal from the encysted piece, whether isolated artificially by section or by the natural process of fragmentation, is similar in all respects to the regulatory development of pieces which reproduce new wholes without encystment. This is shown to be the case by the removal of the cysts from pieces at various stages of the process. In all cases the pieces are simply undergoing regulation. The process within the cyst may, however, be slower than in the unencysted piece, probably because the supply of oxygen within the cysts is less than in the water.

The natural method of asexual reproduction in this species does not then differ essentially in any way from the process of experimental reproduction. The process of fragmentation gives rise to the same conditions in the piece as experimental isolation by section and the further history is the same in both cases.



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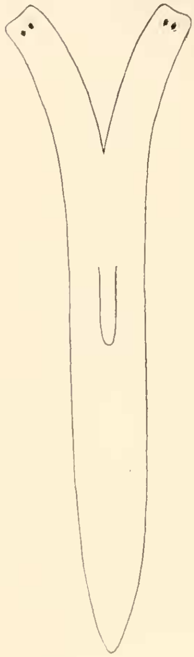

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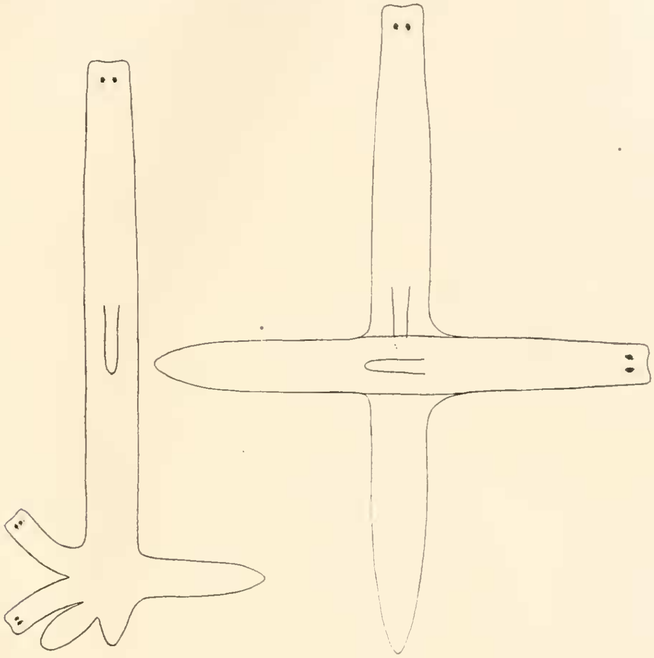
Many teratological forms result from irregularities in fragmentation or incomplete separation. The most common are partial duplications of anterior or posterior regions (Figs. 7 and 8) but various other forms appear. In Fig. 9, for example, a case is shown in which an incompletely separated posterior piece gave rise without encystment to two heads, a tail and two outgrowths of uncertain character, and Fig. 10 shows a case in which two worms with axes at right angles to each other are united by the middle regions of their dorsal surfaces. Ordinarily the larger animal carried the other about on its back as in the figure, the ventral surface of the smaller worm being uppermost. Fig. 11 represents a case of so-called axial heteromorphosis and in Fig. 12 two heads appear at the posterior end of the larger individual and dorsal to them a tail. Evidently new polarities arise very readily in the small pieces which result from fragmentation, probably because the pieces are so short that the



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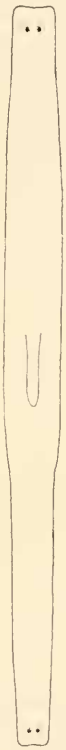
original axial gradient (Child, '13*c*) is practically eliminated and chance differences in the rate of metabolism in different parts of the piece are sufficient to establish new polarities.

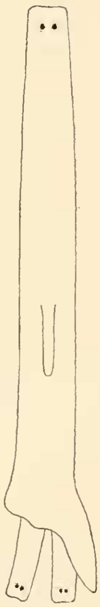
VII. Conclusion.

In *Planaria velata* the individual very evidently undergoes a process of senescence as it grows and either experimental or natural asexual reproduction brings about rejuvenescence. Moreover, the animal apparently returns to essentially the same physiological stage with each generation, for the species is able to persist without sexual reproduction and, as a following paper will show, numerous asexual generations have been bred in the laboratory without any indication of senescence of the stock.

I have shown elsewhere (Child, '11*b*) that the regulation of isolated pieces of *Planaria dorotocephala* brings about rejuvenescence to a greater or less extent, according to the size of the piece, the smaller piece giving rise to an animal which is physiologically younger than that produced by a larger piece. In that species starvation may also be a factor in rejuvenescence. Some experiments on the effect of starvation on *Planaria velata* will be described in another paper. At present it need only be said that the result is the same in both species.



11



12

In my earlier paper on senescence the conclusion was reached that senescence results from the accumulation of structural products of metabolism which constitute in one way or another obstacles to the chemical reactions. The processes of differentiation and growth undoubtedly operate also in another way not considered in the earlier paper, to bring about a decrease in the rate of metabolism per unit of weight or volume. What we are accustomed to call the undifferentiated or embryonic cell represents the general metabolic substratum of the organism. Differentiation consists in the formation and accumulation of certain substances in the cell, some of which constitute more or less permanent structural features. At least certain of the substances composing these structural features are relatively stable under the usual physiological conditions and while certain chemical changes may occur in them, they are not broken down and eliminated to so great an extent as certain other substances. This relative stability must, in fact, be the basis of their persistence as elements of structure. The accumulation of these structural substances within the cell brings about a decrease in the general metabolic activity per unit of weight or volume because it decreases the proportion of the material involved in the general metabolic reactions to the inactive or less active material. The decrease in the proportion of the general metabolic substratum characteristic of the embryonic cell constitutes to some extent a histological criterion of the physiological change in the cell.

In short, the decrease in rate of metabolism per unit of substance, which is characteristic of development and senescence, is undoubtedly due in part to the fact that the proportion of the cell substance concerned in the general metabolic activity is decreasing and the proportion of less active or relatively stable substance is increasing. Changes in the size of the cell or in the size relations of nucleus and cytoplasm (Minot, '08) are not necessary factors in the result.

To what extent the decrease in the rate of metabolism during senescence is due in a given case to actual decrease in the rate of chemical reaction and how far to a decrease in the proportional amount of chemically active or more active substance is often difficult to determine, but it is probable that in some cases, or even in some cells of the individual, the one factor and in others the other is the more important.

As regards *Planaria velata*, the facts are that the rate of metabolism decreases during growth and development and increases when the substances previously accumulated are removed, either by regulatory reorganization, or by starvation. These facts show very clearly that in one way or another the accumulation of material in development decreases the rate of metabolism and its removal brings about an increase in rate. Senescence and rejuvenescence in this species consist essentially, I believe, in these changes.

Summary.

1. After a period of growth and activity *Planaria velata* undergoes fragmentation from the posterior end forward, the fragments encyst and give rise by a process of regulation to whole worms of small size.

2. During the period of growth the worms are undergoing senescence, as the decrease in rate of metabolism indicates, but the small worms which emerge from the cysts are physiologically, as well as morphologically young, possess a high rate of metabolism and are capable of repeating the life cycle.

3. In pieces isolated by section the frequency of encystment increases as the level of the piece becomes more posterior in the body, with decreasing size of the piece, with rising temperature and with increasing age of the animal. The facts indicate that encystment is the result of stimulation. The stimulation may result from section, from fragmentation, from a rise in temperature or from other conditions.

4. The development of the encysted piece into a new whole animal is essentially the same process as the regulatory development of unencysted pieces.

5. This species is able to live for an indefinite number of generations without sexual reproduction. Each new asexual generation represents a return to essentially the same physiological and morphological stage. In other words, senescence leads to reproduction and the process of rejuvenescence in each asexual cycle carries the organism back to the same stage of youth.

Hull Zoölogical Laboratory,
University of Chicago.

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